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Differential responses of red knots, *Calidris canutus*, to perching and flying sparrowhawk, *Accipiter nisus*, models

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According to the threat-sensitive predator avoidance hypothesis, prey should match the intensity of their antipredation response to the degree of threat posed by predators. We used controlled indoor experiments to investigate the ability of red knots to discern between high- and low-threat encounters with a representative predator, the sparrowhawk. The behaviour of knots was compared across three conditions: no predators present (very low predation threat), presentation of a perching sparrowhawk model (low predation threat) and presentation of a gliding sparrowhawk model (high predation threat). In all behavioural parameters measured, red knots showed evidence of discriminating between the different levels of predation risk. Knots responded immediately to the presence of sparrowhawks with escape flights, and the duration of escape flights was longer following the gliding sparrowhawk events than following perching events. Similarly, the proportion of time spent vigilant increased with increasing level of predation threat, while the proportion of time spent feeding decreased. These results show that knots recognize variations in the level of predation threat, and adjust their antipredator responses accordingly. Furthermore, model sparrowhawks were introduced into the experimental arena at similar distances to the knots, which suggests that knots are able to use cues other than distance to predator to gauge the immediate level of threat that a predator poses.
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To reduce their probability of being depredated, animals engage a suite of behaviours, including increasing group size and vigilance levels, and altering habitat usage (Caro 2005). However, increased investment in antipredator behaviours often comes at a cost, because it reduces the time available for, or efficiency of, other behaviours such as foraging, mating or territory defence (Lima & Dill 1990; Caro 2005). Consequently, when determining their allocation to antipredator behaviours, prey must balance the conflicting demands of successfully avoiding predators and engaging in other fitness-enhancing behaviours (Ydenberg & Dill 1986).

The threat-sensitive predator avoidance hypothesis suggests that prey should match the intensity of their antipredation response to the degree of immediate threat posed by the predator (Helfman 1989). Empirical studies have confirmed that in a wide variety of taxa, prey do perceive differences in the level of predation danger and adjust their antipredation responses accordingly (Ydenberg & Dill 1986; Helfman 1989; Lima & Dill 1990; Bulova 1994; Helfman & Winkelman 1997; Laurila et al. 1997; Kats & Dill 1998; Persons & Rypstra 2001). Prey may recognize that different species or classes of predator differ in the threat that they impose (Caro 2005), or may adjust their behaviour according to differences in habitat structure that influence their ability to detect or escape from predators (Lima & Dill 1990; Caro 2005).

Prey may also distinguish between threatening and nonthreatening encounters with individuals of the same predator species. One measure of predation threat is distance, with predators further away imposing less threat than predators nearer to the prey (Ydenberg & Dill 1986). Consistent with this prediction, many animals show increased antipredator response with decreasing distance to predator (Hatch 1970; Helfman 1989; Cavanagh & Griffin 1993; Kleindorfer et al. 2005; Welbergen & Davies 2008). For example, in reed warblers, *Acrocephalus scirpaceus*, the rate of repetition of alarm calls increases with decreasing distance between the nest of the calling individual and the predator (Welbergen & Davies 2008).

There is also evidence that prey are able to recognize more subtle cues of predator lethality, including auditory, chemical, or postural cues (Caro 2005). For a given predator species, not all

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individuals are equally lethal. Both harbour seals, *Phoca vitulina*, and California ground squirrels, *Spermophilus beecheyi beecheyi*, recognize acoustic features of their predators that indicate the degree of threat that they impose (Swaisgood et al. 1999; Deecke et al. 2002). Because predatory individuals are not engaged in hunting all the time, the same individual may not be equally dangerous at all times. Predator behaviour may provide cues as to the current level of threat that they impose (Stankowich & Coss 2007). Although several studies have shown that antipredator responses vary in relation to the behaviour shown by the predator (Robinson 1980; Helfman 1989; Helfman & Winkelman 1997; Edelaar & Wright 2006; Stankowich & Coss 2007), predator behaviour and distance to the prey are often confounded (Cavanagh & Griffin 1993), making it unclear whether prey are using the behaviour of predators or the distance to predators to assess predation risk.

We used controlled indoor experiments to investigate the antipredator behaviour of red knots towards a representative of a major class of predators, the sparrowhawk. We assessed the general response to increased predation risk by comparing the behaviour of knots when no predators were present (control phase) with their behaviour during a period where they experienced two encounters with sparrowhawk models each day (experimental phase). We also investigated whether the behavioural response of knots differed according to more subtle variations in predation threat, while controlling for distance to predator. Each day during the experimental phase, knots were exposed one time each to a perching sparrowhawk model (low threat) and a gliding sparrowhawk model (high threat). We predicted that knots would show a stronger antipredation response to the gliding sparrowhawk model, since this was meant to simulate an attack, and should be perceived as more dangerous than a perching sparrowhawk.

METHODS

Study Subjects

Fifty knots were captured using mist nets on the mudflats of Richel (53°16′57″N, 05°23′82″E) and Simonszand (53°29′28″N, 06°24′19″E) in the Wadden Sea, The Netherlands, on 8 August and 3 September 2005. Prior to experiments, the birds were housed in aviaries at the Royal Netherlands Institute for Sea Research (NIOZ) in four flocks of 12–13 birds. The aviary dimensions were 3.85 × 1.85 and 2.40 m high, and both temperature and photoperiod were set by prevailing conditions. The aviary floors were kept wet with a constant stream of sea water. A tray of running freshwater for drinking and bathing was always present, and the mudsnail, *Hydrobia ulvae*, was provided ad libitum. Prior to experiments, unique combinations of one to four colour flags were applied to the lower legs of all individuals (Barter & Rush 1991). All birds appeared to be in good condition following the experiments, and were released into the wild during low tide at a mudflat near the experimental facility. The experiments complied with Dutch law regarding animal experiments (Dutch Animal Ethics Committee Licence NIOZ 04.04).

Experimental Set-up

We conducted the experiments during 21 August–28 November 2005 at the indoor mudflat facility of the Royal Netherlands Institute for Sea Research (7 × 7 × 3.5 m high). A schematic layout of the experimental mudflat is provided in Fig. 1. During the experiments, a constant photoperiod was implemented (lights on: 0600–2100 hours), with 'moonlight'-mimicking illumination being provided during the dark phase.

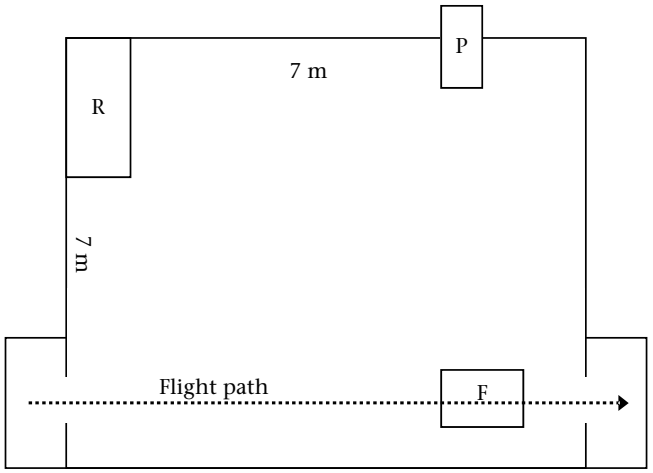

Figure 1. Schematic representation of the experimental arena. The dotted line with arrow indicates the flight path of the gliding sparrowhawk model. The area where the perched sparrowhawk entered the mudflat (P), the location of the food tray (F), and the location of the roosting platform (R) are also indicated.

We conducted eight trials on flocks of six randomly selected birds. Each trial consisted of a 2-day habituation period, followed by a 5-day control and a 5-day experimental period. The order of experimental and control periods was determined at random for each flock, with four flocks receiving the experimental period first, and four flocks receiving the control period first.

During the experimental period of the trials, two event types were used to elevate predation threat. The first consisted of the gliding sparrowhawk model accompanied by digital recordings of red knot alarm calls. The stuffed model glided across one end of the mudflat, passing over the food tray (Fig. 1). Gliding events lasted about 5 s. The second event type involved presenting a model of a perched sparrowhawk supplied with a built-in electromotor that allowed head movement. The perched sparrowhawk model was hidden behind a black curtain except during 'perching' events, when the curtain was lifted and the perched model was rolled into the mudflat arena for 1 min, approximately 0.5 m above the mudflat surface. During the experimental period, 'gliding' and 'perching' events were carried out once each day at unpredictable times between 0930 and 1700 hours with the constraint that events not occur within 90 min of each other in order to allow sufficient time for focal observations between events (see below).

Adopting a set-up with a blank control and two intrusion event types within the experimental treatment enabled testing for discriminatory abilities of prey by comparing three levels of threat: very low threat (control), low threat (perched sparrowhawk model) and high threat (gliding sparrowhawk model).

To clean the mudflat, during all phases of the trials (i.e. habituation, control and experimental), it was flooded briefly (10–30 min) with sea water at 1800 hours. During this time, the birds could rest on an elevated roosting platform. Food was also replaced at this time. Trays of *Hydrobia* were provided in sufficient quantity to allow ad libitum feeding for the following 24 h (see below for additional information on food).

Behavioural Observations

We made 5 min continuous focal observations of each flock member four times per day during both the control and experimental phases of the experiments. Observations were conducted before and after each of the predator events during the experimental period, and at matching time periods during the control

period. The order of observation of individuals was randomized. Focal observations were made from behind a one-way mirror, dictated into a microcassette recorder, and later transcribed using The Observer 3.0 Event Recorder (Noldus Information Technology, Wageningen, the Netherlands). All observations were carried out by K. J. M.

We recorded four behavioural categories (feeding, searching, vigilance and 'others'). Birds were considered to be foraging only when pecking in the food tray. Pecking on the mudflat away from the food tray and walking with the head oriented downwards were both categorized as searching. Vigilance was defined as the bill being parallel to the horizon or higher with accompanying side to side movement of the head. 'Others' includes all behaviours not described above, but most often consisted of resting (motionless with the head up), roosting and preening. Also, following each predator event, the duration of the escape flight was recorded for each bird, as was latency to resume feeding (up to a maximum of 90 min).

Estimated Food Consumption

Throughout the experiments, knots were fed with *Hydrobia* that were caught on 30–31 May 2005 near the Afsluitdijk, The Netherlands (52°58′07″N, 05°06′06″E). *Hydrobia* were stored frozen at −20 °C, and thawed immediately before use. The total wet mass of food provided each day was calculated as the difference between the mass of the feeding tray after filling with *Hydrobia* and the mass of the empty food tray. To estimate the total ash free dry mass (AFDM) of the food provided, we collected and weighed wet mass (WM) of three subsamples (about 60 g each). The subsamples were then dried at 60 °C to constant mass (range 4–7 days), weighed (dry mass, DM), then burned at 560 °C for 4 h and reweighed (ash mass or AM). AFDM of each subsample was calculated as DM − AM. Based on the mean ratio of AFDM:WM of the three subsamples, we calculated the ADFM of the food tray provided.

All food remaining on the food tray after 24 h was collected and weighed at 1800 hours each day. The entire sample was collected, weighed, dried and burned as described above. Because some of the *Hydrobia* meat would be lost via decay over the 24 h period, changes in the AFDM of *Hydrobia* ($AFDM_{provided} - AFDM_{remaining}$) are overestimates of actual consumption by the knots, but provide an index of relative consumption. Three samples were lost before processing, yielding a total of 77 estimates of daily food consumption.

Statistical Analyses

For each focal observation, we calculated the proportion of time spent vigilant, the mean scan duration (s), mean scanning rate (scans/min), the proportion of time spent feeding and the proportion of time spent searching for food. In the experimental phase of experiments, we also calculated the duration of escape flights (s) and the proportion of individuals resuming feeding within 90 min of hawk events.

Data were analysed using linear mixed-effects models (LMEs). LMEs provide estimates of the influence of fixed effects on the mean as well as the influence of random effects on the variance, thereby accounting for the nonindependence of errors resulting from the repeated measures on individuals as well as the repeated measures within flocks (Pinheiro & Bates 2000). LMEs were constructed using R v.2.6.1 ('lme' function of the 'nlme' package of the R statistical computing environment, The R Foundation for Statistical Computing, Vienna, Austria). We tested for differences in escape flight duration between the two hawk event types using models with 'event type' as a fixed effect, and treatment order, flock within treatment order, ID within flock within treatment order, and day within ID within flock within treatment order as random effects ($\sim 1|$ treatment order/flock/ID/day). Differences in the proportion of individuals resuming feeding within 90 min of a predator event were analysed in the same manner; with the exception that 'ID' was not included in the random effects term.

We tested for the effect of predator events on vigilance and foraging behaviour of red knots by including 'treatment' (control or experimental), 'event type' (hawk gliding event or hawk perching event) and observation period (before or after the hawk event) as well as their interactions as fixed effects in the model. 'Event type' was used as a sham factor in the control phase of the experiment to account for the fact that observation times in the control and experimental phase of the experiment were matched for time of day. The random effects structure was the same as described above ($\sim 1|$ treatment order/flock/ID/day). Finally, we tested for an effect of treatment on total daily food consumption using 'treatment' as a fixed effect, and the following structure for random effects: ($\sim 1|$ treatment order/flock/day).

For all models, nonsignificant interactions ($P > 0.10$) were removed in a reverse stepwise manner. We used a significance threshold of 0.10 for interactions because statistical tests have reduced power to detect significant interactions (Littell et al. 1991). We interpreted the significant interactions in lme functions based on the effects sizes estimated by the model (Pinheiro & Bates 2000). All proportions data were arcsine square root transformed before analyses to normalize their distributions. Data on escape flight duration, mean scan duration and scanning rates were Poisson distributed. Therefore, we used ln $(n + 1)$ transformations to normalize their distributions before analyses.

RESULTS

Red knots responded immediately to predator events with escape flights (range 0–116 s). Escape flights were significantly longer following hawk gliding events (mean ± SE = 34.73 ± 1.27 s) than following hawk perching events (28.21 ± 1.27 s) (LME: $F_{1,239} = 63.92$, $P < 0.001$).

Predator events also produced several changes in the activity budgets of red knots. All three indexes of vigilance (proportion of time spent vigilant, mean scan duration, scanning rate) showed changes according to event type, observation period and treatment (see Table 1, Fig. 2a). During the control phase, the proportion of time spent vigilant varied between less than 0.3 and greater than 0.6. There were no consistent effects of event type or observation period on these changes however. The proportion of time spent vigilant was higher during the experimental phase (range 0.6–0.9). During the experimental phase, the proportion of time spent vigilant also increased following hawk gliding events, but not following hawk perching events.

Similar results were observed for mean scan duration (Table 1, Fig. 2b). During the control phase, variation in mean scan duration was not related to either event type, or observation period. Again, overall scan durations were higher during the experimental phase. Scan duration increased following hawk gliding events, but there was no change in mean scan duration following hawk perching events. Changes in scanning rate were opposite to changes in mean scan duration. Again, there was no consistent effect of event type or observation period on scanning rates during the control phase. During the experimental phase, scanning rates did not change following hawk perching events, but decreased following hawk gliding events.

Knots also avoided feeding following predator events (range from 11 min to >90 min following hawk gliding event, and from 1 min to >90 min following hawk perching event). However, the

Table 1
LME results for measures of vigilance: proportion of time spent vigilant, scanning rate (scans/min) and mean scan duration (s)

Source of variation	Effect size	SE	*df*	*F*	*P*
Dependent variable: arcsine square root (proportion of time spent vigilant)					
Treatment*	0.54	0.03	1	383.27	<0.0001
Event type†	0.01	0.03	1	3.39	0.066
Observation period‡	0.13	0.03	1	0.20	0.66
Treatment* × event type†	−0.20	0.05	1	3.43	0.064
Treatment* × observation period‡	−0.39	0.05	1	57.79	<0.0001
Event type† × observation period‡	−0.03	0.05	1	13.55	0.0002
Treatment* × event type† × observation period‡	0.28	0.06	1	20.03	<0.0001
Dependent variable: ln (scans/min + 1)					
Treatment*	−0.03	0.00	1	62.63	<0.0001
Event type†	0.01	0.00	1	19.94	<0.0001
Observation period‡	0.01	0.00	1	29.08	<0.0001
Treatment* × event type†	0.01	0.01	1	0.14	0.71
Treatment* × observation period‡	0.03	0.01	1	15.16	0.0001
Event type† × observation period‡	0.00	0.01	1	14.60	0.0001
Treatment* × event type† × observation period‡	−0.02	0.01	1	7.98	0.0048
Dependent variable: ln (scan duration (s) + 1)					
Treatment*	1.67	0.10	1	386.38	<0.0001
Event type†	−0.22	0.10	1	20.05	<0.0001
Observation period‡	0.04	0.10	1	45.25	<0.0001
Treatment* × event type†	−0.62	0.14	1	0.88	0.35
Treatment* × observation period‡	−1.35	0.14	1	73.87	<0.0001
Event type† × observation period‡	0.11	0.14	1	45.59	<0.0001
Treatment* × event type† × observation period‡	1.06	0.19	1	30.09	<0.0001

All data were transformed before analyses to normalize their distributions.
* 'Control' was the reference for treatment in the model.
† 'Gliding' was the reference for event type in the model.
‡ 'Post-' was the reference for observation period in the model.

mean ± SE proportion of birds feeding within 90 min of a hawk perching event was nearly double the proportion feeding within 90 min of a hawk gliding event (0.76 ± 0.08 versus 0.42 ± 0.08, respectively), and this difference was significant (LME: $F_{1,39} = 27.24$, $P < 0.001$).

The reduced tendency to feed was also reflected in the amount of time devoted to feeding and searching for food on the mudflat (away from the food tray) (Table 2). Overall, the proportion of time spent feeding was lower during the experimental phase than during the control phase (mean ± SE difference 0.04 ± 0.00; Fig. 3a). During the experimental phase, birds also reduced the proportion of time spent feeding following predator events, with a larger decrease in feeding following hawk gliding events than following hawk perching events. During the control phase, there was no effect of observation period or event type on the proportion of time spent foraging.

Results for the proportion of time allocated to searching were similar. Overall, birds spent less time searching during the experimental phase than during the control phase (Table 2, Fig. 3b). During the experimental phase, birds reduced the proportion of time spent searching for food following hawk gliding events, but not following hawk perching events. In contrast, during the control period, there was no effect of observation period or event type on the amount of time spent searching.

The reduced time feeding and searching for food resulted in changes in food consumption during trials. Knots consumed significantly less during the experimental phase (LME: $F_{1,36} = 12.87$, $P = 0.001$). The average ± SE food consumption during the control phase was 164.40 ± 7.06 g AFDM, compared with 139.72 ± 9.86 g AFDM during the experimental phase, a mean reduction of 15%.

In each of the models presented above, the random effect of 'day' accounted for a large proportion of the variation in the data sets. In contrast, 'treatment order' had a consistently small effect, indicating that the response of red knots to our treatments was not conditional on the order in which they received the treatment phases. Variance components for all random effects are summarized in Table 3.

DISCUSSION

We tested whether red knots adjust the intensity of their anti-predation response according to the degree of threat posed by predators by comparing their behaviour across three levels of predation threat: no predators present (very low predation threat), presentation of a perching sparrowhawk model (low predation threat) and presentation of a gliding sparrowhawk model (high predation threat). In all behavioural parameters measured (escape flights, vigilance and feeding), red knots appeared to discriminate between the different levels of predation risk. The presence of the sparrowhawk model prompted escape flights by the knots, and the duration of escape flights was longer following the gliding sparrowhawk events than following the perching sparrowhawk events. Predator events also resulted in an increased proportion of time spent vigilant, and a decreased proportion of time spent feeding. The magnitude of these effects was greater following gliding sparrowhawk events.

Knots responded immediately to the presence of sparrowhawks in the experimental mudflat with escape flights. Distance moved is a commonly used metric to assess a prey's perception of predation risk (Taylor & Knight 2003; Stankowich 2008), with greater distance moved being associated with higher perceived predation risk. However, because the knots were confined to the experimental mudflat, the net distance they could move was restricted. Therefore, we recorded the duration of escape flights following predator events because the duration of escape behaviour is also correlated with perceived predation risk (Nebel & Ydenberg 2005; Stankowich & Coss 2007). Escape flights were longer following the gliding sparrowhawk events than following perching events, consistent with red knots perceiving the hawk

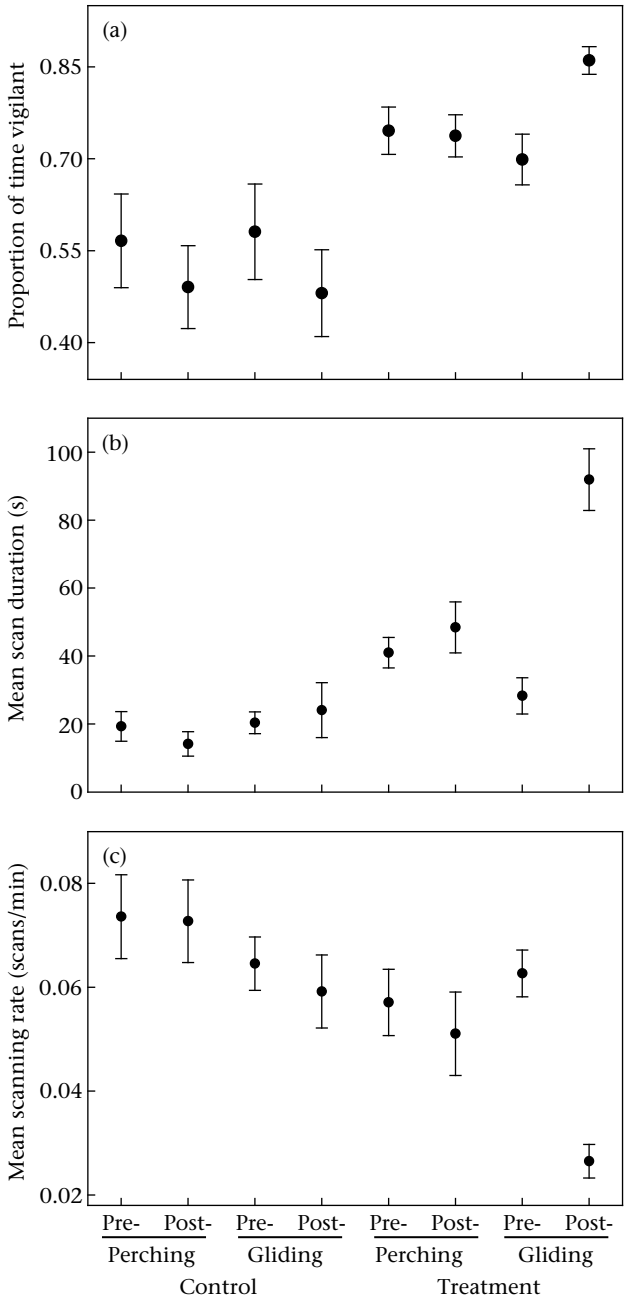

Figure 2. Changes in (a) proportion of time devoted to vigilance, (b) mean scan duration and (c) mean scanning rate in relation to treatment, event type and observation period. Note that raw values are depicted, while models were constructed for transformed data. Values indicated are means ± 1 SE.

gliding events as imposing a greater level of threat than the perching events.

Following hawk gliding events, knots increased the proportion of time spent vigilant. Their patterns of vigilance also changed, with vigilance bouts lasting longer, but occurring less frequently following hawk gliding events. In contrast, there was no change in the time allocated to vigilance following hawk perching events, although knots did alter their vigilance strategy following hawk perching events. As with hawk gliding events, scan duration increased and scanning rate decreased following hawk perching events. However, these trends were of smaller magnitude than those for hawk gliding events.

Encounters with predators often result in an immediate interruption of feeding behaviour (Lima & Dill 1990). Latency to resume feeding can depend on a variety of factors, including the hunger level of the prey, but is also strongly influenced by predation danger (Lima & Dill 1990; Caro 2005), with latency to resume feeding increasing with increased perceived predation danger (Lima & Dill 1990; Cooper 1998; van der Veen 2002; Martín & López 2005). More birds resumed feeding within 90 min of a hawk perching event (>75%) compared with hawk gliding events (~40%). These results therefore suggest that knots perceived the gliding hawk events as imposing a greater threat than the perching hawk events. Alternative explanations, such as hunger level, are unlikely to account for these results because there should be no systematic differences in hunger level associated with the two predator event types given that event types and times were randomly assigned.

The results of latency to resume feeding are also reflected in the analyses of the proportion of time spent feeding. While knots reduced their investment in feeding behaviour following both types of predator events, the reduction was greater following hawk gliding events. These results are also consistent with knots perceiving a gliding hawk as a greater predation threat than a perched sparrowhawk. Alternatively, the greater aversion to feeding following hawk gliding events may not reflect an aversion for the behaviour itself, but may be the result of avoidance with the location in the experimental arena where the food tray was located, because it lay under the flight path of the gliding sparrowhawk. However, the proportion of time spent searching for food outside of the food tray showed very similar patterns to those for feeding, suggesting that the reduction in feeding was not merely a consequence of avoiding the location where the food tray was located, but did reflect a reduced tendency to forage.

Behavioural changes induced by encounters with predators may not be long-lasting, in which case, observations of behaviour immediately following predator events may provide overestimates of the long-term effect of predators on the behaviour of prey (Lima & Bednekoff 1999). Our results do show strong immediate responses to predator events, particularly following hawk gliding events. However, comparisons of behavioural measures prior to encounters with the model predator during the experimental phase, and all measures taken during the control phase, indicate that there were also long-term changes in the behaviour of knots induced by encounters with the two types of model predator. Overall vigilance levels (proportion of time spent vigilant and mean scan duration) were greater during the experimental phase, and both proportion of time feeding and proportion of time searching were lower. Measures of food consumption throughout the trials confirmed that the reduction in feeding behaviour continued throughout the experimental phase. Although predator events lasted less than 2 min of a 15 h foraging period, they resulted in a 15% reduction in food consumption during the experimental phase.

One possible criticism of our experimental design is that the control phase did not provide a true control. The hawk events during the experimental phase not only increased perceived predation danger, but also created a disturbance, and red knots are known to be sensitive to disturbances (Koolhaas et al. 1993; McGowan et al. 2002). However, under natural conditions, encounters with predators would provide both a disturbance and an increased perceived risk of predation to prey; therefore, we believe our design does provide meaningful estimates of the response of knots to encounters with predators. In a similar study, van den Hout et al. (2006) compared the antipredation response of ruddy turnstones, *Arenaria interpres*, to a raptor model versus a gull

Table 2
LME results for proportion of time spent feeding and proportion of time spent searching for food outside the food tray

Source of variation	Effect size	SE	*df*	*F*	*P*
Dependent variable: arcsine square root (proportion of time feeding)					
Treatment*	−0.21	0.02	1	158.15	<0.0001
Event type†	0.06	0.02	1	9.27	0.0024
Observation period‡	0.04	0.02	1	55.71	<0.0001
Treatment* × event type†	0.04	0.03	1	2.44	0.12
Treatment* × observation period‡	0.19	0.03	1	31.50	<0.0001
Event type × observation period‡	−0.03	0.03	1	22.00	<0.0001
Treatment* × event type† × observation period‡	−0.14	0.04	1	10.50	0.0012
Dependent variable: arcsine square root (proportion of time spent searching)					
Treatment*	−0.09	0.01	1	151.84	<0.0001
Event type†	0.07	0.01	1	16.37	0.0001
Observation period‡	0.04	0.01	1	14.67	0.0001
Treatment* × event type†	−0.02	0.01	1	2.76	0.097
Treatment* × observation period‡	0.04	0.01	1	6.91	0.0086
Event type† × observation period‡	−0.06	0.01	1	16.09	0.0001

Proportion data were transformed before analyses to normalize their distributions.
* 'Control' was the reference for treatment in the model.
† 'Gliding' was the reference for event type in the model.
‡ 'Post-' was the reference for observation period in the model.

model. They found that the gull model had no consistent effect on the turnstones relative to their starting values prior to the experiments, while the raptor model had a strong effect. These results suggest that the major factor driving the response in the prey is increased perceived predation risk, and not disturbance. Furthermore, in our study, the duration of the hawk perching events (1 min) greatly exceeded the duration of the hawk gliding events (about 5 s). Thus, even if knots are more sensitive to disturbance than are turnstones, the greater response of red knots to hawk gliding events cannot be explained by greater levels of disturbance associated with those events, but is consistent with the gliding sparrowhawk events being perceived as more threatening than perching sparrowhawk events.

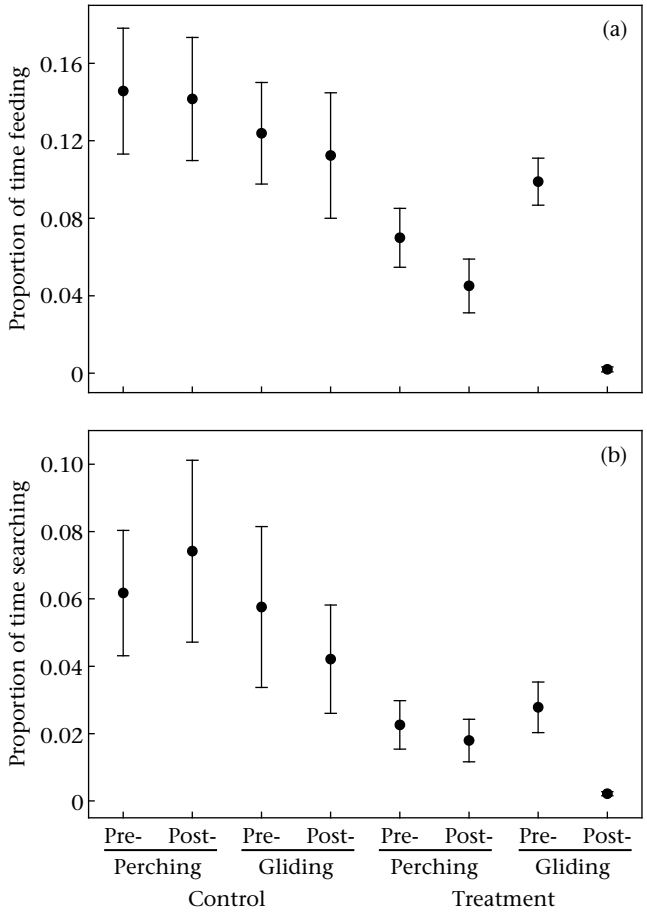

Figure 3. Changes in the proportion of time spent (a) feeding and (b) searching, in relation to treatment, event type and observation period. Note that raw values are depicted, while models were constructed for transformed data. Values indicated are means ± 1 SE.

The investment in vigilance behaviour was high throughout the experiments, including the control phase, which was meant to simulate very low predation threat. This may be due to easy access to ad libitum food, freeing up more time for vigilance behaviours. However, the high levels of vigilance may also have been due to knots having had high perceived danger throughout the experiment, including the control phase, which may have resulted either from the daily disturbances that knots experienced when food was replenished and the mudflat was cleaned, or from the structure of the experimental mudflat. Shorebirds are often hunted by predators that rely on obstructive cover to conceal their attacks (Lazarus & Symonds 1992; Pomeroy et al. 2006). The walls surrounding the experimental mudflat may have been perceived as providing obstructive cover for such predators.

Our results show graded responses by red knots to increasing levels of predation danger. Previous studies have suggested that prey are able to use the behaviour of predators to gauge predation risk, however, studies in birds have often confounded predator behaviour and distance to predator (Hatch 1970; Cavanagh & Griffin 1993; Edelaar & Wright 2006). In our study, the stronger responses to the gliding predator events cannot be explained by proximity between the knots and the sparrowhawk model, because the experimental arena was a relatively small arena (7 × 7 m), and distances between the knots and the predators during the two event types were similar. Thus, knots were able to use cues other than distance to evaluate predation risk. The 'high threat' gliding events were accompanied by recordings of red knot alarm calls. Therefore, we cannot conclude to what extent the behaviour of the gliding sparrowhawk versus the presence of alarm calls contributed to the increased perception of risk. Nevertheless, our results clearly show that knots do recognize variations in the level of predation threat, and adjust their antipredator responses accordingly.

Table 3
Variance components for model random effects

Model dependent variable	Treatment order	Group	ID	Day
Arcsine square root (prop. time vigilant)	0.00	10.94	3.87	82.09
Ln (scanning rate (scans/min) + 1)	1.03	0.11	5.71	90.51
Ln (scan duration (s) + 1)	0.00	5.62	4.90	87.08
Arcsine square root (prop. time feeding)	0.00	6.42	4.09	84.26
Arcsine square root (prop. time searching)	0.00	10.49	5.22	80.10
Ln (escape flight duration (s) + 1)	0.00	27.20	0.00	72.80
Arcsine square root (prop. resuming feeding)	0.00	8.59	N/A	57.11
Food consumption (g)	5.51	0	N/A	94.49

For details of model fixed effects, see Tables 1 and 2.

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